ON THE RENAL ORGANS OF NUCULA NUCLEUS, LINN.

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PLATE X.

The anatomy of many members of the Protobranchia has been investigated with considerable care during the last ten years, and has been found to show in many points indications of the retention in these forms of a very primitive and unspecialized condition.

Amongst the organs distinguished by primitive characteristics are the organs of Bojanus, and they, especially in their relations with the genital ducts, are without doubt of very great interest. In 1891 Pelseneer 1 drew attention to the fact that in Nucula nucleus, Leda pella, and Solenomya togata the genital duet communicated with the exterior through the organ of Bojanus, opening into that organ, not, as it does in several other lamellibranchs of a low type, just within the external orifice, but close to the pericardium. The importance of this announcement is obvious, for this arrangement points towards a yet earlier stage in the specialization of the lamellibranch colom. in which the genital, pericardiae, and renal exclomic cavities were in open communication, and the genital products escaped, as they now do in Aplacophora, through the pericardium and nephridia—a stage but little in advance of the condition characteristic of Annelids, in which the genital products are formed at certain points upon the walls of a general colomic cavity, and escape from that eavity through peritoneal funnels comparable to the Molluscan kidney.² This observation was later on confirmed by Stempell,3 so far as concerns Solenomya, but apparently the like condition does not occur in the members of the Nuculidæ and Ledidæ examined by him 4 or by Drew. 5 For instance,

¹ P. Pelseneer, "Contribution à l'étude des Lamellibranches": Arch. de Biol., tom. xi (1891), p. 165.

² Goodrich, "On the Caslom, Genital Ducts, and Nephridia": Quart. Journ. Micro. Sci., vol. xxxvii (1895), p. 477.

Stempell, "Zur Anatomie von Solenomya togata, Poli": Zool. Jahrb., Bd. xiii (1900), p. 141.

⁴ Stempell, "Beiträge zur Kenntniss der Nuculiden": Zool. Jahrb. (Fauna Chilensis), Bd. i (1898), p. 398.

⁵ Drew, "Some Observations on the Habits, Anatomy, and Embryology of members of the Protobranchia": Anat. Anz., Bd. xv (1899), p. 503. "The Life-History of Nucula delphinodonta (Mighels)": Quart. Journ. Micro. Sci., vol. xliv (1941), p. 380.

in Yollia limatulu the genital duct is described and figured by Drew as opening into the organ of Bojanus close to its external orifice, as he says it also does in Nucula proxima and N. delphinodonta; although in the latter case he is not prepared to say that it has not also a connection with either the pericardium, or the reno-pericardiac duct. In Leda sulcata, L. pella, and Malletia Chilensis, Stempell describes the passage of the genital duct into the organ of Bojanus close to its external opening, but notes in addition in Leda sulcata an open communication between the pericardiac arm of the kidney (close to the pericardium) and the uro-genital cloaca formed by the union of the genital duct and ureter. In Malletia this 'gonopericardiac' duct is represented by a solid cord. Pelseneer, in a second paper, revises his former description of these parts in Nucula, Leda, and Solenomya, and states that in these forms, as well as in Yoldia hyperborea, the genital duet opens into the pericardiac arm of the kidney, where it passes into the reno-pericardiac duct, but that a secondary connection leads directly from this point of confluence of the two organs to the external renal opening—a statement that may well be a reverse interpretation of a condition similar to that recorded by Stempell for Leda.

In face of these somewhat conflicting accounts, further investigation into the relationship between the genital ducts and the organ of Bojanus in these genera is much needed. But, as may be gathered from the want of unanimity in the descriptions of even the same species, these parts, from their delicacy and close apposition, are extremely difficult to disentangle with any certainty except in really well-preserved material. Amongst several indifferently preserved series of sections of Nucula nucleus, I was fortunate enough to get one in exceptionally good condition, so that I am in a position to add yet another description of the anatomy of these organs, which, so far as

the specimen is concerned, should be reliable.

In any transverse section, taken close in front of the nephrostomes, the longitudinally pleated genital duct (Pl. X, Figs. 1 and 2, od.)—in this particular instance the oviduct—is found lying on either side below the pericardium, between the body-wall and the excurrent arm of the kidney and above the cerebro-visceral connective. From this level it can be traced backwards, below and to the outer side of the reno-pericardiac duct, the latter being tightly wedged in between it and the excurrent arm of the organ of Bojanus. The duct now turns inwards towards the mesial plane, meets the antero-lateral wall of the ureter above the cerebro-visceral connective, and opens into it, converting the distal part of the ureter into a uro-genital cloaca (Fig. 2, ug.c.). The reno-pericardiac duct, as just stated, lies for the first part of its course upon the dorsal surface of the oviduct. As it makes its way towards the deep surface of the ureter to pass behind it to the pericardiac arm of the kidney, it occupies the angle formed by the union of the genital duct and the ureter, and

Pelseneer, Recherches Moll. archaïques: Mém. Cour. Acad. Roy. Belgique, t. lvii (1899 [i.e. 1901]), p. 62.

at this point opens into the uro-genital cloaca, just dorsal to the opening of the genital duct (Figs. 2 and 3, x). The opening is a simple perforation of the apposed walls of the duct and cloaca, and is in no way drawn out to form such a tubular connection as that described by Stempell in this position in Leda. There is no doubt whatever that the opening of the genital duct is into the uro-genital cloaca in front of and below this 'gono-pericardiac' pore, and not, as Pelseneer finds in his specimens, into the reno-pericardiac duct. meaning of this connection is somewhat obscure. It is certainly not an artifact, for it is present and perfectly symmetrically on both sides, besides having been noted in several other genera. Nor is it easy to see by what physiological need such an opening would be called into being. It would no doubt serve to rapidly remove products of excretion from the pericardial cavity, were such present; but in these lowly forms the pericardial epithelium is not yet specialized to form an adventitious excretory organ (Grobben's glands, Keber's organ). It is most probably, as Stempell suggests, the original passage of the genital duct into the kidney, in course of being supplanted by the direct path through the uro-genital cloaca.

To turn now to the anatomy of the organs of Bojanus (Figs. 1 and 4), which, although not so important as the connection between the kidney and the genital duct, is yet of some considerable interest. In the descriptions of these organs in the Protobranchia given by Pelseneer, Stempell, and Drew, there is a general similarity. Typically, in the Nuculidæ and Ledidæ each organ is tubular and U-shaped, with the convexity of the U directed forward (it is turned backward, according to Pelseneer, in Nucula nucleus), and with the pericardiac and external openings lying nearly in the same transverse plane at the free end of either arm of the U. The tube of which the kidney consists is generally very long (Leda, Yoldia), and is more or less sacculated or The arborescence is specially marked in arborescent and coiled. The distal part of the excurrent arm is smooth without The entire organ, except the reno-pericardiac duct and sacculations. the wreter, is lined by excretory epithelium. In most cases (Leda sulcata, L. pella, Malletia Chilensis, Yoldia hyperborea) there is an open

communication between the pericardiac arms of either side.

From a comparison of three series of transverse sections of *Nucula nucleus*, it appears that in all essentials the organs of Bojanus in this species resemble those of other Nuculidæ and Ledidæ. They are in the first place lined throughout (except for the reno-pericardiac duct and nreter) by excretory epithelium. Each is U-shaped, with the convexity of the U directed forward. But the limbs of the U are very short, far shorter than as figured by Stempell in *Leda sulcata* or described by Drew in *Yoldia*, and are not coiled, but give off many sacculations and arborescent processes.

The hinder end of the pericardiac arm of the kidney lies below the posterior parts of the pericardium at some little distance in front of the posterior adductor. It opens freely into its fellow of the opposite side. In front it stretches forward and diagonally outwards below the pericardium, and gives off several arborescent processes. The most

important of these are: one, extending upwards and inwards beside the rectum and between it and a coil of the intestine (Fig. 3, arb. 1), and two that run downwards and forwards, embracing the hindermost gut coil (Fig. 4, arb. 2). Shortly after giving off these diverticula the pericardiac arm of the organ bends back upon itself to form the excurrent arm (Figs. 3 and 4, exc. a.). The latter is quite short, somewhat inflated, and without arborescent processes. Near its hinder end it opens to the exterior below the attachment of the gill by a short uro-genital cloaca that passes above the cerebro-visceral connective. From the convexity of the U several arborescent processes are given off, and ramify amongst the viscera, extending some way alongside the stomach (Fig. 1, arb. 3). The reno-pericardiac duct is of some length. It opens into the pericardium by a nephrostome (Figs. 1 and 2, neph.) situated in the floor on a level with the hinder margin of the ventricle, and slightly in advance of the external renal orifice. From the nephrostome it passes backwards, internal to the ureter, to open into a little diverticulum in the floor of the pericardiac arm of the kidney, on a level with the anterior limit of the communication between the two organs.

The renal epithelium, which lines all parts of the organ except the reno-pericardiac duct and ureter, consists of large rounded cells, containing vacuoles and a few concretions. The cells are provided with a few long straggling cilia. The reno-pericardiac duct consists of a low columnar epithelium covered with remarkably long coarse cilia. The epithelium of the ureter is strongly ciliated, and a similar ciliated epithelium extends for some distance upon the body-surface, around

the uro-genital opening.

Without doubt these kidneys are of a very primitive type, as shown particularly by their continuous excretory lining. There has been some little discussion as to whether the U shape with anterior convexity is also a primitive feature. It seems that as regards Nucula this condition may very well be a modification, indirectly produced by mechanical means, of what was admittedly in all probability the original form of lamellibranch kidney, a simple tube leading directly from the pericardium to the exterior. In Nucula, and, I believe, in other protobranchs, the stomach is remarkable for its relatively great size, and extends backwards between and below the anterior horns of the pericardium. The pericardium, on the other hand, is peculiarly short and broad, forming a crescentic sac with forwardly directed horns. The heart likewise is antero-posteriorly compressed, with long spindleshaped auricles that run forwards to the extremities of the pericardial This peculiar form of the pericardium and heart can be most rationally explained as the result of pressure exerted by the enlarged stomach, whereby the central part of the pericardium has been pushed backwards and compressed, while the lateral parts are held fast in front by the attachment of the auricles to the efferent vessel in the gill axis. The nephrostomes, which lie not far on either side of the mesial line of the pericardium, would share in its backward migration, and as the reno-pericardiac ducts pass outwards in front of the ureters, the latter also would be involved in the backward movement,

leaving the middle part of the tube as the forward convexity of the U. Thus the U formation in this case, and in *Solenomya* and lamellibranchs in general, is probably due to very different causes. For in the latter it appears that the anterior end of the pericardium with the nephrostomes has been the fixed point, and that the middle part of the renal tube has been drawn backwards by the general backward growth of the body.

EXPLANATION OF PLATE X.

Fig. 1.—Diagram of the right organ of Bojanus and neighbouring parts of *Nucula nucleus*, seen from the side.

, 2.—Diagram showing the relation of the oviduct and organ of Bojanus.

,, 3.—Part of transverse section of Nucula nucleus, passing through the opening between the reno-pericardiac duct and the uro-genital cloaca.

4.—Diagram of the organs of Bojanus viewed from above.

arb. 1-3. arborescent processes of the organ of Bojanus.

cv.c. cerebro-visceral connection.

exc.a. excurrent arm of the organ of Bojanus.

int. intestine.

neph. nephrostome.

od. oviduct.

pc., pc'. pericardial cavity and cut edge of pericardial floor.

pc.a. pericardial arm of the organ of Bojanus.

rect. rectum.

rp.d. reno-pericardial duct.

ug.c. uro-genital cloaca.

x. opening between rp.d. and ug.c.